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SHORT COMMUNICATION

Changes in phenology and abundance of suction-trapped Diptera from a farmland site in the UK over four decades

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Abstract. 1. Recently documented insect declines have caused major concerns and an increased interest in studies using long-term population-monitoring data.

2. Samples from a 12.2-m suction trap were used to examine trends in phenology and abundance of Diptera over four decades.

3. The timing of peak flight has advanced by an average of 17 days, from 23 July in 1974 to 6 July in 2014.

4. The abundance of flies has decreased by 37% over the studied period (from April to September), and peak abundance has decreased by 48%. The flight period has started earlier in recent years, and in 2014, the number of flies was higher in spring until the 31st of May than in 1974. Possible causes and impacts of these changes are discussed.

Key words. Climate change, insect decline, long-term population trends, Rothamsted suction traps, U.K..

Introduction

Studies suggest that there has been a recent decline in both the biomass (Hallmann *et al.*, 2017; Macgregor *et al.*, 2019) and diversity of insects (Seibold *et al.*, 2019). Multiple reasons for this have been proposed, but the main causes are likely to be habitat loss and degradation, environmental toxins, and climate change (Wagner, 2020). It is possible to determine the effects of individual stressors at the species level under experimental conditions. In the field, however, these drivers work together, and the overall effects are difficult to predict, especially for whole insect communities (Robinet & Roques, 2010; Damien & Tougeron, 2019; Montgomery *et al.*, 2020; Didham *et al.*, 2020).

While most studies suggest that the overall effects of habitat loss and degradation, as well as of pesticide use, are negative, the effects that climate change can have on different organisms cannot be described so easily. In temperate regions, many organisms demonstrate substantial phenological trends over time, which are often attributed to climate change (Robinet & Roques, 2010). Well-studied responses to warming temperatures are, for example, advanced spring flight periods, which have been shown in butterflies (Roy & Sparks, 2000) and aphids (Harrington *et al.*, 2007) in the U.K. Many butterfly and moth species develop additional generations per year in response to warming temperatures (Altermatt, 2010). At the same time, the distribution of many species in the northern hemisphere is shifting to the north (Thomas, 2010). Where interdependent species respond differently to climate change, phenological mismatch may occur (Kharouba *et al.*, 2018). This phenomenon, together with the spread of invasive species due to facilitation by warming temperatures (Robinet & Roques, 2010; Renault *et al.*, 2018), can pose problems for endemic species and may disrupt whole ecosystems (Thackeray *et al.*, 2010; Martay *et al.*, 2017). Besides the direct effects of warming on insects, associated phenomena also have an impact on them. For example, snow cover in winter is reduced, which can have negative effects on the overwintering survival of insects due to greater exposure to low air temperatures (Bale & Hayward, 2010; Harris *et al.*, 2019). At the same time, extreme climate events, such as heavy rainfall, storms, and droughts, are increasing, altering the living conditions and possibly exceeding the physical limits of species (e.g. Hoffmann *et al.*, 2013).

The analysis of long-term phenological and population data is valuable in understanding the effects of climate change on

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species assemblages (Renner & Zohner, 2018). For insects, such data are often only available for high-profile taxa (Saunders *et al.*, 2020), and it has been shown that these are not always representative of other taxonomic groups (Bell *et al.*, 2020; Outhwaite *et al.*, 2020). Insects form a vital component of most terrestrial and freshwater ecosystems (Hershey *et al.*, 2010; Mooney *et al.*, 2010; Vidal & Murphy, 2019). Therefore, studying changes in their phenology and abundance is a prerequisite to understanding ecosystem responses to environmental changes. Changes in phenology and abundance in response to environmental changes vary with species and spatial scale (Bell *et al.*, 2018; Frik *et al.*, 2020), and generalisation has proved elusive (Diez *et al.*, 2012; Davies, 2019).

Dipterans form important components of most terrestrial and freshwater food webs (Wallace *et al.*, 2015; Raitif *et al.*, 2019), and they provide many vital ecosystem functions, such as decomposition (Benbow *et al.*, 2019), predation of other arthropods (Werner & Pont, 2003; Westcott & Lavigne, 2019), and pollination (Ssymank *et al.*, 2008; Orford *et al.*, 2015). It has been shown that flies are the most abundant aerial insects in the U.K. (Shortall *et al.*, 2009), but they have been studied less in relation to long-term changes in phenology and abundance, largely because of the paucity of relevant data. The network of suction traps coordinated by the Rothamsted Insect Survey (Storkey *et al.*, 2016) was established primarily to study the dynamics of aphids. All trapped insects are retained, offering a unique opportunity to study long-term changes in any insect taxa that occur in the trap samples in sufficient abundance for statistical analysis (e.g. Sanders *et al.*, 2019). In this study, we use these samples to investigate how the phenology and abundance of flies has changed over 41 years from 1974 to 2014.

Material and methods

Trapping and study design

Flies were sampled using a 12.2 m-tall suction trap (Fig. S1) that collects aerial biomass through sampling 50 m^3 air per minute (Macaulay *et al.*, 1988). The samples investigated came from the trap located at Rothamsted in Harpenden, U.K. (lat: 51.806997°, long: −0.360091°). The landscape surrounding the trap is mainly agricultural. Land use has not changed significantly during the period of the study. The trap is emptied daily (weekly in winter), and arthropods are stored in 95% ethanol with 5% glycerol. Due to the large number of samples (>12 000) and the time required to count and identify all flies in one sample (on average, ca. 40 dipteran individuals per sample), a subsampling strategy was applied, covering a time frame from 1974 to 2014, with every fourth year investigated except for 1978, for which several samples were missing. Within each year, samples on every fourth day from the beginning of April to the end of September were investigated by counting all brachyceran flies, as well as the two nematoceran families Bibionidae (March flies) and Simuliidae (black flies). All specimens were returned to ethanol storage to facilitate future analyses.

Meteorological data were recorded in a Stevenson screen at Rothamsted, part of the UK Met Office network of weather stations. We selected as potential explanatory variables minimum temperature (°C) (T_{min}); wind speed ($m\,s^{-1}$) (windspeed); and temperature range (°C) (T_{range}), which is the difference between the minimum and maximum temperatures on a given day. It is well known that temperature (up to an optimum value) is positively correlated with the flight activity of insects, which are all poikilothermic (Taylor, 1963). It is also known that the flight readiness of most insects decreases at increased wind speeds (Møller, 2013), even though some species use wind to assist dispersal (Chapman *et al.*, 2015). Temperature and wind speed may have differing importance for insects depending on their time of flight (Peng *et al.*, 1992).

Statistical analysis

We used Generalised Additive Models (GAMs) as the relationship between the response variable, that is, the number of flies on a certain date, and explanatory variables, that is, T_{min}, windspeed, T_{range}, day within the year (Y_{day}), and year (Y), was expected to not always be linear. We checked all parameters for compliance with a normal distribution; only windspeed required a square root transformation to meet this requirement. For visualisation and analysis of the population dynamics, we smoothed the meteorological daily data individually using a 2D smoother with a thin-plate regression spline. These smoothed meteorological variables were subsequently used for a new prediction.

Pearson correlation coefficients for all explanatory variables were lower than ±0.33, indicating that multicollinearity among variables was minimal. GAMs were specified within the packages gamlss (Rigby & Stasinopoulos, 2005) and gamlss.add (Stasinopoulos *et al.*, 2016). To identify the optimal distribution, we compared models with 31 different distributions (Table S1). Furthermore, we visually inspected the model fit and the residual pattern. The beta negative binomial distribution with a log-link function was chosen as it had the lowest aikake information criterion (AIC) and second lowest bayesian information criterion (BIC) values of all models. For the interaction between Y_{day} and Y, we specified a 2D smoother with a thin-plate regression spline. To test whether the additive interaction term for Y and Y_{day} improved the model, we compared the AIC of a model with and without the interaction specified. The other explanatory variables (T_{min}, T_{range}, windspeed) were expected to have a linear relationship with the response variable, so they were retained in the model as linear predictors. Their significance was tested by single-term deletion and comparison of the models' AICs. All analyses and visualisations were carried out using R Core Team (2019).

Results

A total of 17 959 flies belonging to 28 brachyceran families and two nematoceran families were counted and identified to family level. Of 30 dipteran families, 4 accounted for 80.3% of the abundance, namely, Phoridae, Bibionidae, Chloropidae, and Sphaeroceridae (Table S2). The model (Table 1) indicated a shift in the main occurrence of flies towards earlier dates (Fig. 1). While the highest number of flies was predicted to be on 23rd July in 1974, in recent years, this advanced by 17 days to 6th

Table 1. Model specifications of the beta negative binomial generalised additive model for the number of flies.

Parameter	Estimate	SE	t-value	*P*
Intercept	4.385	0.164	26.768	<0.001
T_{min}	−0.034	0.013	−2.566	0.011
T_{range}	0.145	0.016	9.330	<0.001
Windspeed	−0.237	0.030	−7.801	<0.001

Number of observations on the fit: 436. Degrees of freedom for the fit: 14.627. Residual degrees of freedom: 421.373.

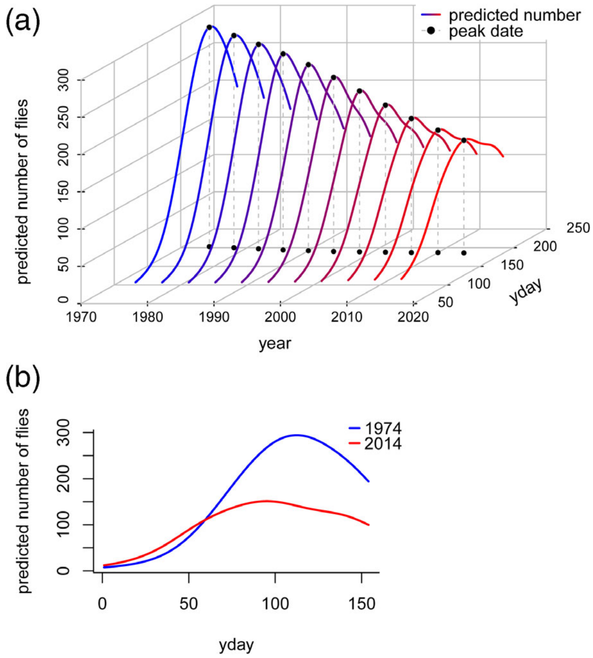

Fig. 1. (a) Diptera abundance development showing the interaction between year and day within year as predicted by the generalised additive model (bold line). Dots on the bottom plane indicate the date of maximum number, showing that the peak shifts towards earlier dates. The curve flattens towards recent years, resulting in a decrease of abundance on the peak date and indicating a prolonged season. (b) Diptera abundance development from April to September in the first (1974) and last year (2014) of the study. The graph shows an overall abundance decrease, except in spring, before the beginning of June. [Colour figure can be viewed at wileyonlinelibrary.com].

July. The average number of flies per day decreased from 98 in 1974 to 62 in 2014, resulting in an overall loss of 37%. The occurrence curve flattened and broadened. Despite numbers in the main flight peak decreasing (from 293 flies in 1974 to 152 flies in 2014, a decline of 48%), the flight period started earlier, and the number of flies was higher in 2014 than in 1974 until the 31st of May. The Pearson correlation between the observed and predicted values based on the original meteorological values was 0.38, t = 8.57, df = 434, *P*-value = <0.001.

Discussion

The shift of the main occurrence towards earlier dates is in accordance with other studies from temperate regions (Bartomeus *et al.*, 2011; Thackeray *et al.*, 2016; Cohen *et al.*, 2018). As many fly species fulfil ecosystem services such as pollination (Ssymank *et al.*, 2008; Orford *et al.*, 2015), the shift in phenology might lead to a temporal mismatch between pollinators and the opening of flowers due to different phenological responses, as has been shown in other systems (Schenk *et al.*, 2018). Other beneficial biotic interactions might also be desynchronised as some fly species are natural enemies of crop pests (e.g. Asilidae, Empididae, Tachinidae), and others are involved in nutrient cycling as detritivores (e.g. Bibionidae, Drosophilidae, Phoridae, Sarcophagidae).

The most abundant families exhibit a broad spectrum of life histories. While for the most abundant family, Phoridae, various life cycles are known, the larvae of Bibionidae and Sphaeroceridae feed mainly on decaying organic matter and are considered microbial grazers (Marshall, 2012). Chloropidae and Agromyzidae are leaf miners and include some economically important pest species (Marshall, 2012).

Besides the shift towards earlier peak flight, there was a decreasing trend in peak abundance even though Shortall *et al.* (2009), who analysed the biomass of all invertebrates of the same samples, did not show a decrease in biomass. Aerial biomass did not change significantly over this period. This might partly be due to the extended period of activity, as well as the fact that most flies in the suction trap samples, even though abundant, are very small. By weight, they are dwarfed by social wasps and macro moths. For example, the trap at Rothamsted has a significant *Vespula* population in most years.

Flies are an important food resource for many higher trophic levels, like predatory insects such as dragonflies (Kaunisto *et al.*, 2017), and birds (Holland *et al.*, 2006). The lower abundance is expected to have negative impacts on them in turn. In particular, insectivorous bird species are affected by population declines over the last few decades (Bowler *et al.*, 2019), and there is a close correlation between these declines and the decline of insects at the same time (Møller, 2019). Flies make up a significant proportion of the food of aerial insectivorous birds (Orłowski & Karg, 2013). It is probable that the decline in the abundance of flies will have cascading effects on biological communities (Martay *et al.*, 2017).

Further work is required to determine whether these results are unique to this single trap or are representative of trends occurring on a wider scale. Another goal is to estimate the biomass by weighing individuals of some taxa, so it can be understood why the numbers of flies were decreasing although there was no change in total insect biomass. More work is required to determine the factors (climate change, land use, or otherwise) driving these changes. In order to better understand the changes in autumn, we need to study them over a longer period of time, at best the whole year. It would be a great gain in knowledge to identify the flies to species level. That would make it possible to untangle population dynamics shifts of species from changes in overall community composition.

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Author contributions

C. R. Shortall and R. Harrington designed the project; S. Grabener collected data; J. Oldeland and S. Grabener conducted statistical analysis; and S. Grabener, R. Harrington, J. Oldeland, and C. R. Shortall wrote the paper.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. A 12.2 m-tall suction trap located at Rothamsted in Harpenden, U.K.

Table S1. AIC and BIC values for the fitted models. Ranking is based on AIC.

Table S2. Number and percentage of flies per family.

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